

# Multiscale analysis: Fisher-Wright diffusions with rare mutations and selection, logistic branching system

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## Abstract

We study two types of stochastic processes, a mean-field spatial system of interacting Fisher-Wright diffusions with an inferior and an advantageous type with rare mutation (inferior to advantageous) and a (mean-field) spatial system of supercritical branching random walks with an additional deathrate which is quadratic in the local number of particles. The former describes a standard two-type population under selection, mutation, the latter models describe a population under scarce resources causing additional death at high local population intensity. Geographic space is modelled by  $\{1, \dots, N\}$ . The first process starts in an initial state with only the inferior type present or an exchangeable configuration and the second one with a single initial particle. This material is a special case of the theory developed in [DGsel].

We study the behaviour in two time windows, first between time 0 and  $T$  and secondly after a large time when in the Fisher-Wright model the rare mutants succeed respectively in the branching random walk the particle population reaches a positive spatial intensity. It is shown that the second phase for both models sets in after time  $\alpha^{-1} \log N$ , if  $N$  is the size of geographic space and  $N^{-1}$  the rare mutation rate and  $\alpha \in (0, \infty)$  depends on the other parameters. We identify the limit dynamics in both time windows and for both models as a nonlinear Markov dynamic (McKean-Vlasov dynamic) respectively a corresponding random entrance law from time  $-\infty$  of this dynamic.

Finally we explain that the two processes are just two sides of the very same coin, a fact arising from duality, in particular the particle model generates the genealogy of the Fisher-Wright diffusions with selection and mutation. We discuss the extension of this duality relation to a multitype model with more than two types.

**Keywords:** Fisher-Wright diffusion, selection and mutation, branching random walk with logistic death, duality, McKean-Vlasov equation, random entrance law.

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## Contents

<b>0</b>	<b>Introduction</b>	<b>3</b>
0.1	Motivation and background . . . . .	3
0.2	Outline . . . . .	4
<b>1</b>	<b>The Fisher-Wright model with rare mutation and selection</b>	<b>4</b>
1.1	A two-type mean-field diffusion model and its description . . . . .	4
1.2	Two time windows for the spread of the advantageous type . . . . .	6
1.3	The early time window as $N \rightarrow \infty$ . . . . .	7
1.4	The late time window as $N \rightarrow \infty$ . . . . .	10
<b>2</b>	<b>A logistic branching random walk and its growth</b>	<b>14</b>
2.1	The logistic branching particle model . . . . .	14
2.2	The early time window as $N \rightarrow \infty$ . . . . .	15
2.3	The droplet expansion and Crump-Mode-Jagers processes . . . . .	16
2.4	Time point of emergence as $N \rightarrow \infty$ . . . . .	18
2.5	The late time window as $N \rightarrow \infty$ . . . . .	19
<b>3</b>	<b>The duality relation</b>	<b>22</b>
3.1	A classical duality formula . . . . .	22
3.2	The genealogy and duality . . . . .	23
3.3	The dual for general type space . . . . .	23
3.3.1	A multitype model . . . . .	23
3.3.2	The dual with selection . . . . .	24
3.3.3	The dual with migration, selection and mutation . . . . .	27
3.4	Outlook on set-valued duals . . . . .	28

## 0 Introduction

### 0.1 Motivation and background

We study here features of the longtime behavior of two models for the stochastic evolution of populations, the classical (mean-field) spatial version of a system of interacting Fisher-Wright diffusions with selection and mutation on the one hand and a logistic spatial branching particle model both on geographic space  $\{1, \dots, N\}$ . We shall later explain the mathematical relation between them.

*Fisher-Wright model.* This process comes from population genetics and models a population of individuals of two types evolving under migration, resampling, selection and mutation. It is the many individual limit of a discrete model. Migration here means individuals move in geographic space, resampling that pairs are replaced by an offspring pair each choosing a parent at random and adopting the parents type, mutation is a spontaneous change of type of an individual and under selection the choice of the parent in the resampling event is biased according to the parents' fitness.

Here we are particularly concerned with a situation where we have an inferior type and an advantageous type. The case we are interested in is that the mutation rate from inferior to advantageous is very small so that in finite time we expect  $O(1)$ -many mutations in all of space as space gets large. We want to follow the population through the *emergence* and *fixation* of the whole population in the advantageous type.

*Logistic branching model.* Here we consider a population of particles which migrate in space, have offspring at a certain rate  $s$ , die with a certain rate (all particles act independently) but here the risk of death is at a rate increasing with the population size of the site and being zero for one particle. The latter mechanism induces an interaction of the families, which therefore do not evolve anymore independently of each other.

Here for this model we want to see how the population starting from one particle spreads and eventually colonizes the whole space as time evolves, meaning that a positive spatial intensity is reached and a local equilibrium situation arises where locally the process neither becomes extinct nor grows and becomes infinitely large as  $t \rightarrow \infty$ . This is in contrast to the behaviour of classical branching models with their survival versus extinction dichotomy in finite geographic space and reflects the limited resources in a given colony.

*McKean-Vlasov equation and random entrance laws.* The techniques we use to study the questions raised above for two models is the mean-field limit, where we choose migration to occur according to the uniform distribution on  $\{1, \dots, N\}$  and rare mutation having rate  $N^{-1}$  and where we let  $N \rightarrow \infty$ . As limit dynamics a nonlinear Markov process of the type first introduced by McKean [Mc] arises, i.e. an evolution with a generator where the parameters depend on the current state of the process *and* on the current law. The transition probabilities solve the *McKean-Vlasov equation* which has a similar structure to the equations introduced by Vlasov to describe the dynamics of a plasma consisting of charged particles with long-range interaction. A similar scenario holds for the branching particle system.

The first rigorous and systematic analysis of mean-field models and resulting McKean-Vlasov dynamics is Gärtner's fundamental paper in 1988 [Gar] which established the existence and uniqueness of weak solutions for a general class of McKean-Vlasov equations and the associated non-linear martingale problems but under the condition that the diffusion matrix is *strictly* positive definite. Hence it does not cover the case dealt with in this paper due to the fact that for the Fisher Wright diffusions the diffusion function vanishes at the boundary.

We must also extend here the methodology of the McKean-Vlasov equation further in order to describe the limiting behaviour in different time windows. In order to also consider a late time

window we need first of all to introduce the notion of an entrance law from time  $-\infty$  (our time parameter has the form  $T_N + t$ ,  $t \in \mathbb{R}$  and  $T_N \rightarrow \infty$  as  $N \rightarrow \infty$ ) but since in the initial time phase some randomness is involved (rare mutation respectively very small early particle intensity) we even have to work with *random entrance laws* to the McKean-Vlasov equation.

*Duality.* The mathematical structure which relates our two models is the fact that they are in duality, i.e. expectations of certain functionals under one dynamic are given by expectations of appropriate functionals under the other dynamic with the time direction reversed. This will be explained in detail later on.

The duality relation which we present here is a special case of a broader new duality theory for multitype models, which allows a historical and genealogical interpretation and which has been developed in [DGsel] covering much more general situations than we can discuss here. More information on the particle system can be found in [Schirm10].

**Remark 1** *In the framework just sketched we can analyse the features of the population as described above. If one wants to adapt a more realistic model for geographic space the mean-field limit has to be replaced by the hierarchical mean-field limit for which the present analysis is a key ingredient. Then it is possible to study asymptotically two-dimensional geographic space via its approximations by the hierarchical group of order  $N$  and  $N \rightarrow \infty$ . This also allows us to investigate the question of universality of the behaviour. All this is carried out in [DGsel] and we refer the interested reader to this paper.*

## 0.2 Outline

In section 1 we shall present the Fisher-Wright model, in section 2 the logistic branching model and in section 3 the connection between both via duality.

# 1 The Fisher-Wright model with rare mutation and selection: Behaviour in two time windows

Here we introduce the Fisher-Wright model, some relevant time windows, state its properties in two time windows and consider the McKean-Vlasov limit for the model in five separate subsections.

## 1.1 A two-type mean-field diffusion model and its description

We study a population with two types, one of low and the other of high fitness, where initially all the population is of the lower type but by a rare mutation the advantageous type appears and spreads with time. The population is described specifying the proportion of the type 1 (the inferior) in every spatial colony.

Formally we look at a process  $(X^N(t))_{t \geq 0}$  with  $N \in \mathbb{N}$  of the following form:

$$(0.1) \quad X^N(t) = ((x_1^N(i, t), x_2^N(i, t)); i = 1, \dots, N),$$

$$(0.2) \quad x_1^N(i, 0) = 1, \quad i = 1, \dots, N,$$

satisfying the well-known SSDE:

$$(0.3) \quad dx_1^N(i, t) = c(\bar{x}_1^N(t) - x_1^N(i, t))dt - s x_1^N(i, t)x_2^N(i, t)dt - \frac{m}{L}x_1^N(i, t)dt \\ + \sqrt{d \cdot x_1^N(i, t)x_2^N(i, t)}dw_1(i, t),$$

$$(0.4) \quad dx_2^N(i, t) = c(\bar{x}_2^N(t) - x_2^N(i, t))dt + s x_1^N(i, t)x_2^N(i, t)dt + \frac{m}{L}x_1^N(i, t)dt \\ + \sqrt{d \cdot x_1^N(i, t)x_2^N(i, t)}dw_2(i, t),$$

where  $w_2(i, t) = -w_1(i, t)$  and  $\{(w_1(i, t))_{t \geq 0}, i = 1, \dots, N\}$  are i.i.d. Brownian motions,  $m, d, s, L \in (0, \infty)$  and

$$(0.5) \quad \bar{x}_\ell^N(t) = \frac{1}{N}\hat{x}_\ell^N(t) \text{ with } \ell = 1, 2, \quad \hat{x}_\ell^N(t) = \sum_{i=1}^N x_\ell^N(i, t).$$

Later we will use the parameter of mutation strength and size of geographic space satisfying

$$(0.6) \quad L = N.$$

We can study this system in various ways, *locally* by looking at a  $K$  tagged sites

$$(0.7) \quad (x_\ell^N(1, t), \dots, x_\ell^N(K, t)), \quad \ell = 1, 2$$

or *globally* using the concept of the empirical measure of the complete population:

$$(0.8) \quad \Xi_N(t) := \frac{1}{N} \sum_{i=1}^N \delta_{(x_1^N(i, t), x_2^N(i, t))} \in \mathcal{P}(\mathcal{P}(\{1, 2\}))$$

and the empirical measure process of either type:

$$(0.9) \quad \Xi_N(t, \ell) := \frac{1}{N} \sum_{i=1}^N \delta_{x_\ell^N(i, t)} \in \mathcal{P}([0, 1]), \quad \ell = 1, 2.$$

Note that since  $x_1^N(i, t) + x_2^N(i, t) = 1$  it suffices in the case of two types to know one component of the pair in (0.9), the other is then determined by this condition. Then for two types we can effectively replace  $\mathcal{P}(\mathcal{P}(\{1, 2\}))$  by  $\mathcal{P}([0, 1])$  as states of the empirical measure.

However since very soon rare mutants appear somewhere in space they are present for  $t > 0$ , but of course the set of sites where they are visible is *sparse*, we have to find a way to describe this small subset where the advantageous type appears. One (global) way is to consider the process

$$(0.10) \quad \hat{x}_\ell^N(t) = \sum_{i=1}^N x_\ell^N(i, t) \text{ with } \ell = 1, 2,$$

but this way we lose the internal structure of the droplet of sites with advantageous types of substantial mass. In order to keep track of the sparse set of sites at which nontrivial mass appears we will give a random label to each site and define the following *atomic-measure-valued process*.

We assign independent of the process a point  $a(j)$  randomly in  $[0, 1]$  to each site  $j \in \{1, \dots, N\}$ , that is, we define the collection

$$(0.11) \quad \{a(j), \quad j = 1, \dots, N\} \text{ i.i.d. uniform on } [0, 1].$$

We then associate with our process and a realization of the random labels a measure-valued process on  $\mathcal{P}([0, 1])$ , which we denote by  $(\mathfrak{I}_t^{N,m})_{t \geq 0}$  where

$$(0.12) \quad \mathfrak{I}_t^{N,m} = \sum_{j=1}^N x_2^N(j, t) \delta_{a(j)}.$$

The process  $(\mathfrak{I}_t^{N,m})_{t \geq 0}$  describes the essential features of the advantageous population.

## 1.2 Two time windows for the spread of the advantageous type

The first question now is how the advantageous type develops in finite time and the second on what time scale does the advantageous type take over the whole population meaning we want to identify a time  $T_{N,L}$  after which the advantageous type has positive spatial intensity. A key role is played by space and the fact that the dynamic is random and not deterministic as in the scenario looked at by [Bu]. So we look at the cases  $N = 1$ ,  $N$  large and  $L$  small,  $d = 0$ ,  $d > 0$ .

*Case  $N = 1$  (nonspatial)*

Here we find the time scales in which we emerge  $(T_{N,L} = T_L)$  as  $L \rightarrow \infty$  to be

$$(0.13) \quad O(s^{-1} \log L) \text{ for } d = 0,$$

$$(0.14) \quad O(L) \text{ for } d > 0.$$

This qualitative difference is essentially due to the fact that in the stochastic model the diffusion can hit 0 by sheer random effects, while in the deterministic model the advantageous type expands exponentially fast leading to a  $\log L$  time scale.

*Case  $N \gg 1$  (large spatial model)*

Here we take  $L = N(T_{N,L} = T_N)$  and then we find also in the deterministic case the time scale  $s^{-1} \log N$ , but also now in the stochastic model,  $d > 0$ , we have a time period  $\alpha^{-1} \log N$  but now the  $\alpha$  will turn out to be strictly smaller than  $s$ . In the sequel we analyse the latter case in more detail and identify the constant  $\alpha$ .

**Remark 2** *The relation  $L = N^{-1}$  is appropriate if one considers the mean-field model which in the hierarchical mean-field limit is a potential-theoretic analogue of two-dimensional space as  $N \rightarrow \infty$ , see [DGsel] and for which migration, mutation, selection are all three together important.*

The task is now to describe the system in the limit  $N \rightarrow \infty$  in two time windows:

- times of order 1 after starting:  $(X^N(t))_{t \geq 0}$
- times  $\alpha^{-1} \log N$  after starting:  $(X^N(\alpha^{-1} \log N + t)^+)_{t \in \mathbb{R}}$ .

In the first window the evolution of the small advantageous droplet is of primary interest, in other words the process  $\mathfrak{I}^{N,m}$ , while in the second case when the droplet covers a positive proportion of the whole space, the system is best described by the empirical measure  $\Xi_N$  (see 0.8) or the tagged sample see (0.7).

### 1.3 The early time window as $N \rightarrow \infty$

Here we want to describe (1) the evolution of the atomic measure-valued process  $\mathfrak{J}^{N,m}$  in the limit  $N \rightarrow \infty$  over times in some finite interval and (2) the limit  $N \rightarrow \infty$  of the dynamic of the empirical measure.

#### (1) Droplet evolution

During the early times there will be a finite random number of sites where the advantageous type has mass exceeding some prescribed  $\varepsilon > 0$ . Therefore as  $N \rightarrow \infty$  we expect a limiting evolution of  $(\mathfrak{J}_t^N)_{t \geq 0}$ . First of all we can show

**Proposition 1.1** (*Limiting droplet dynamic*)

As  $N \rightarrow \infty$

$$(0.15) \quad \mathcal{L}[(\mathfrak{J}_t^{N,m})_{t \geq 0}] \xrightarrow[N \rightarrow \infty]{} \mathcal{L}[(\mathfrak{J}_t^m)_{t \geq 0}],$$

in the sense of convergence of continuous  $\mathcal{M}_a([0, 1])$ -valued processes where the set of atomic measures  $\mathcal{M}_a([0, 1])$  is equipped with the weak atomic topology. The topology is introduced in [EK4] and we don't touch this further here.  $\square$

To identify the limit evolution  $\mathfrak{J}^m$  we need a bit of classical excursion theory (compare [PY], section 3, [Hu]).

**Lemma 1.2** (*Single site: entrance and excursion laws*)

(a) Let  $c > 0, d > 0, s > 0$ . Then 0 is an exit boundary for the the Fisher-Wright diffusion

$$(0.16) \quad dx(t) = -cx(t)dt + sx(t)(1-x(t))dt + \sqrt{d \cdot x(t)(1-x(t))}dw(t),$$

which then has a  $\sigma$ -finite entrance law from state 0 at time 0, the  $\sigma$ -finite excursion law

$$(0.17) \quad \mathbb{Q} = \mathbb{Q}^{c,d,s}$$

on

$$(0.18) \quad W_0 := \{w \in C([0, \infty), \mathbb{R}^+), w(0) = 0, w(t) > 0 \text{ for } 0 < t < \zeta \text{ for some } \zeta \in (0, \infty)\}.$$

(b) Moreover, denoting by  $P^\varepsilon$  the law of the process started with  $w(0) = \varepsilon$  and  $\varepsilon > 0, \mathbb{Q}$  is given by:

$$(0.19) \quad \mathbb{Q}(\cdot) = \lim_{\varepsilon \rightarrow 0} \frac{P^\varepsilon(\cdot)}{S(\varepsilon)},$$

where  $S(\cdot)$  is the scale function of the diffusion (0.16), defined by the relation,

$$(0.20) \quad P_\varepsilon(T_\eta < \infty) = \frac{S(\varepsilon)}{S(\eta)}, \quad 0 < \varepsilon < \eta < \infty,$$

where  $T_\eta$  is the first hitting time of  $\eta$ .

For the Fisher-Wright diffusion  $S$  is given by (cf. [RW], V28)) the initial value problem:

$$(0.21) \quad S(0) = 0, \frac{dS}{dx} = \frac{e^{-2sx}}{(1-x)^{2c}},$$

so that

$$(0.22) \quad \lim_{\varepsilon \rightarrow 0} \frac{S(\varepsilon)}{\varepsilon} = 1.$$

(c) The measure  $\mathbb{Q}$  is  $\sigma$ -finite, namely for any  $\eta > 0, \zeta$  as in (0.18),

$$(0.23) \quad \mathbb{Q}(\{w : \zeta(w) > \eta\}) < \infty,$$

$$(0.24) \quad \mathbb{Q}(\sup_t(w(t)) > \eta) = \mathbb{Q}(T_\eta < \infty) = \frac{1}{S(\eta)} \longrightarrow \infty \text{ as } \eta \rightarrow 0,$$

and

$$(0.25) \quad \int_0^1 x \mathbb{Q}(\sup_t(w(t)) \in dx) = \infty. \quad \square$$

Now the limit ( $N \rightarrow \infty$ ) droplet dynamic  $\mathfrak{I}^m$  can be identified as follows.

**Proposition 1.3** (A continuous atomic-measure-valued Markov process)

Let  $N(ds, da, du, dw)$  be a Poisson random measure on (recall (0.18) for  $W_0$ )

$$(0.26) \quad [0, \infty) \times [0, 1] \times [0, \infty) \times W_0,$$

with intensity measure

$$(0.27) \quad ds da du \mathbb{Q}(dw),$$

where  $\mathbb{Q}$  is the single site excursion law defined in (0.19) in Lemma 1.2.

Then the following two properties hold.

(a) The stochastic integral equation for  $(\mathfrak{I}_t^m)_{t \geq 0}$  given as

$$(0.28) \quad \mathfrak{I}_t^m = \int_0^t \int_{[0,1]} \int_0^{q(s,a)} \int_{W_0} w(t-s) \delta_a N(ds, da, du, dw), \quad t \geq 0,$$

where  $q(s, a)$  denotes the non-negative predictable function

$$(0.29) \quad q(s, a) := (m + c \mathfrak{I}_{s-}^m([0, 1])),$$

has a unique continuous  $\mathcal{M}_a([0, 1])$ -valued solution, which equals  $(\mathfrak{I}_t^m)_{t \geq 0}$  from equation (0.15).

(b) The process  $(\mathfrak{I}_t^m)_{t \geq 0}$  has the following properties:

- branching property (the process is like a branching process with immigration)
- the mass of each atom observed from the time of its creation follows an excursion from zero generated from the excursion law  $\mathbb{Q}$  (see (0.19)),
- new excursions are produced at time  $t$  at rate

$$(0.30) \quad m + c \mathfrak{I}_t^m([0, 1]),$$

- each new excursion produces an atom located at a point  $a \in [0, 1]$  chosen according to the uniform distribution on  $[0, 1]$ ,
- at each  $t$  and  $\varepsilon > 0$  there are at most finitely many atoms of size  $\geq \varepsilon$ .  $\square$

(2) *McKean-Vlasov equation for limiting empirical measure.*

Turn now to the global description of the complete population by the empirical measure. In the limit  $N \rightarrow \infty$  the evolution of the empirical measure in a finite time window is given by the McKean-Vlasov limit of our system, but of course it is trivial, that is, totally concentrated on type 1 if the given initial state has this property. This is however different at late times. Consider therefore the above system (0.1)-(0.4) of  $N$  interacting sites with type space  $\mathbb{K} = \{1, 2\}$  starting at time  $t = 0$  from a product measure (that is, i.i.d. initial values at the  $N$  sites). The *basic McKean-Vlasov limit* (cf. [DG99], Theorem 9) says that if we start initially in an i.i.d. distribution, then

$$(0.31) \quad \{\Xi_N(t)\}_{0 \leq t \leq T} \xrightarrow[N \rightarrow \infty]{} \{\mathcal{L}_t\}_{0 \leq t \leq T},$$

where the  $\mathcal{P}(\mathcal{P}(\{1, 2\}))$ -valued *deterministic* path  $\{\mathcal{L}_t\}_{0 \leq t \leq T}$  is the law of a *nonlinear* Markov process solving a *forward* equation, namely the unique weak solution of the *McKean-Vlasov equation*:

$$(0.32) \quad \frac{d\mathcal{L}_t}{dt} = (L_t^{\mathcal{L}_t})^* \mathcal{L}_t,$$

where for  $\pi \in \mathcal{P}(\mathcal{P}(\mathbb{K}))$ ,  $L^\pi$  is given by the generator of the process given by the evolution of type 1 in (0.34) below, (and  $\pi = m(t)$ ) and the  $*$  indicates the adjoint of an operator mapping from a dense subspace of  $C_b(E, \mathbb{R})$  into  $C_b(E, \mathbb{R})$  w.r.t. the pairing of  $\mathcal{P}(E)$  and  $C_b(E, \mathbb{R})$  given by the integral of the function with respect to the measure.

As pointed out above in (0.9), in the special case of the type set  $\{1, 2\}$ , we can simplify by considering the frequency of type 2 only and by reformulating (0.32) living on  $\mathcal{P}(\mathcal{P}(\{1, 2\}))$  in terms of  $\mathcal{L}_t(2) \in \mathcal{P}[0, 1]$ . This we carry out now.

Namely we note that given the mean-curve

$$(0.33) \quad m(t) = \int_{[0,1]} y \mathcal{L}_t(2)(dy),$$

the process  $(\mathcal{L}_t(2))_{t \geq 0}$  is the *law* of the solution of (i.e. the unique weak solution) the SDE:

$$(0.34) \quad dy(t) = c(m(t) - y(t))dt + sy(t)(1 - y(t))dt + \sqrt{dy(t)(1 - y(t))}dw(t),$$

with  $w$  being standard BM. Then informally  $(\mathcal{L}_t)_{t \geq 0}$  corresponds to the solution of the nonlinear diffusion equation. Namely for  $t > 0$ ,  $\mathcal{L}_t(2)(\cdot)$  is absolutely continuous and for

$$(0.35) \quad \mathcal{L}_t(2)(dx) = u(t, x)dx \in \mathcal{P}([0, 1])$$

the evolution equation of the density  $u(t, \cdot)$  is given by:

$$(0.36) \quad \frac{\partial}{\partial t} u(t, x) = -c \frac{\partial}{\partial x} \left\{ \int_{[0,1]} y u(t, y) dy - x \right\} u(t, x) - s \frac{\partial}{\partial x} (x(1-x)u(t, x)) + \frac{d}{2} \frac{\partial^2}{\partial x^2} (x(1-x)u(t, x)).$$

We have the following basic property for the McKean-Vlasov equation.

**Proposition 1.4** (*McKean-Vlasov equation and its solution*)

(a) *Given the initial state  $\mu_0 \in \mathcal{P}([0, 1])$  there exists a unique solution*

$$(0.37) \quad \mathcal{L}_t(2)(dx) = \mu_t(dx), \quad t \geq t_0$$

*to (0.32) with initial condition  $\mathcal{L}_{t_0}(2) = \mu_0$ .*

(b) *If  $s > 0$  and  $\int_{[0,1]} x \mu_{t_0}(dx) > 0$ , then this solution satisfies:*

$$(0.38) \quad \lim_{t \rightarrow \infty} \mathcal{L}_t(2)(dx) = \delta_1(dx). \quad \square$$

### 1.4 The late time window as $N \rightarrow \infty$

In the late time window we see (global) *emergence* and then *fixation* of the advantageous type.

(1) Emergence times. Here we begin by studying the emergence by identifying the time of emergence and of fixation of the advantageous type as follows.

**Proposition 1.5** (*Macroscopic emergence and fixation times*)

(a) (*Emergence-time*)

There exists a constant  $\alpha$  with:

$$(0.39) \quad 0 < \alpha < s,$$

such that if  $T_N = \frac{1}{\alpha} \log N$ , then for  $t \in \mathbb{R}$  and asymptotically as  $N \rightarrow \infty$  type 2 is present at times  $T_N + t$ , i.e. there exists a  $\varepsilon > 0$  such that for every  $i$ ,

$$(0.40) \quad \liminf_{N \rightarrow \infty} P[x_2^N(i, T_N + t) > \varepsilon] > 0,$$

and type 2 is not present earlier, namely for  $1 > \varepsilon > 0$ :

$$(0.41) \quad \lim_{t \rightarrow -\infty} \limsup_{N \rightarrow \infty} [P(x_1^N(i, T_N + t) < 1 - \varepsilon)] = 0.$$

(b) (*Fixation time*)

After emergence the fixation occurs in times  $O(1)$  as  $N \rightarrow \infty$ , i.e. for any  $\varepsilon > 0$ ,  $i \in \mathbb{N}$

$$(0.42) \quad \lim_{t \rightarrow \infty} \limsup_{N \rightarrow \infty} P[x_1^N(i, T_N + t) > \varepsilon] = 0. \quad \square$$

**Corollary 1.6** (*Emergence and fixation times of spatial density*)

The relations (0.40), (0.41) and (0.42) hold for  $\bar{x}_2^N$  respectively  $\bar{x}_1^N$  as well.  $\square$

We can identify the parameter  $\alpha$  as follows from the droplet growth behaviour.

**Proposition 1.7** (*Long-time growth behavior of  $\mathfrak{I}_t^m$* )

Assume that  $m > 0$ . Then the following growth behavior of  $\mathfrak{I}^m$  holds.

(a) There exists  $\alpha^*$  such that the following limit exists

$$(0.43) \quad \lim_{t \rightarrow \infty} e^{-\alpha^* t} E[\mathfrak{I}_t^m([0, 1])] \in (0, \infty),$$

with (here  $\alpha$  is from (0.39))

$$(0.44) \quad \alpha^* = \alpha, \text{ where } \alpha \text{ is given below in (0.93)}$$

$$(0.45) \quad e^{-\alpha t} \mathfrak{I}_t^m([0, 1]) \xrightarrow[t \rightarrow \infty]{} \mathcal{W}^* \text{ in probability, } 0 < \mathcal{W}^* < \infty \text{ a.s..}$$

(b) The growth factor in the exponential is truly random:

$$(0.46) \quad 0 < \text{Var}[\lim_{t \rightarrow \infty} e^{-\alpha t} \mathfrak{I}_t^m([0, 1])] < \infty. \quad \square$$

**Remark 3** The random variable  $\mathcal{W}^*$  reflects the growth of  $\mathfrak{I}_t^m([0, 1])$  in the beginning, as is the case in a supercritical branching process and hence  $\mathcal{E}^* = \alpha^{-1} \log \mathcal{W}^*$  can be viewed as the random time shift of that exponential  $e^{\alpha t}$  which matches the total mass of  $\mathfrak{I}_t^m$  for large  $t$ .

**Remark 4** *Even though one might think that for small mass of the advantageous type this expands at the rate  $e^{st}$ , this is not the case due to the stochastic effects leading to a subtle interplay between the parameters  $s, d$  and  $c$  resulting in  $\alpha^* = \alpha < s$ .*

(2) *Fixation dynamic.* We now understand the preemergence situation and the time of emergence and fixation. In order to describe the whole dynamics of *macroscopic fixation*, we consider the limiting distributions of the empirical measure-valued processes in a second time window  $(\alpha^{-1} \log N + t)^+$ ,  $t \in \mathbb{R}$ . Define (we suppress the truncation in the notation below)

$$(0.47) \quad \Xi_N^{\log, \alpha}(t) := \frac{1}{N} \sum_{i=1}^N \delta_{(x_1^N(i, \frac{\log N}{\alpha} + t), x_2^N(i, \frac{\log N}{\alpha} + t))}, \quad t \in \mathbb{R}, \quad (\Xi_N^{\log, \alpha}(t) \in \mathcal{P}(\mathcal{P}(\mathbb{K})))$$

and then the two empirical marginals are given as

$$(0.48) \quad \Xi_N^{\log, \alpha}(t, \ell) := \frac{1}{N} \sum_{i=1}^N \delta_{x_\ell^N(i, \frac{\log N}{\alpha} + t)}, \quad \ell = 1, 2 \text{ and } t \in \mathbb{R}, \quad (\Xi_N^{\log, \alpha}(t, \ell) \in \mathcal{P}([0, 1])).$$

Note that for each  $t$  and given  $\ell$  the latter is a random measure on  $[0, 1]$ . Furthermore we have the representation of the empirical mean of type 2 as follows:

$$(0.49) \quad \bar{x}_2^N(\frac{\log N}{\alpha} + t) = \int_{[0, 1]} x \Xi_N^{\log, \alpha}(t, 2)(dx).$$

Since we consider the limits of systems observed in the interval  $\text{const} \cdot \log N + [-\frac{T}{2}, \frac{T}{2}]$  with  $T$  any positive number, that is setting  $t_0(N) = \text{const} \cdot \log N - \frac{T}{2}$ , we need to identify entrance laws for the process from  $-\infty$  (by considering  $T \rightarrow \infty$ ) out of the state concentrated on type 1 with certain additional properties.

The next main result is on the fixation process, saying that  $\Xi_N^{\log, \alpha}$  converges as  $N \rightarrow \infty$  and that the limit can be explicitly identified as a random McKean-Vlasov entrance law from  $-\infty$ , a concept we explain next.

**Definition 1.8** (*Entrance law from  $t = -\infty$* )

*We say in the two-type case that a probability measure-valued function  $\mathcal{L} : \mathbb{R} \rightarrow \mathcal{P}([0, 1])$ , is an entrance law at  $-\infty$  starting from type 1 if  $(\mathcal{L}_t)_{t \in (-\infty, \infty)}$  is such that  $\mathcal{L}_t$  solves the McKean-Vlasov equation (0.32) and  $\mathcal{L}_t \rightarrow \delta_1$  as  $t \rightarrow -\infty$ .  $\square$*

We will indeed establish that the emergence of rare mutants gives rise to “*random*” solutions of the McKean-Vlasov dynamics. In particular we will show that the limiting empirical measures at times of the form  $C \log N + t$  are *random* probability measures on  $[0, 1]$  and therefore given by sequences of  $[0, 1]$ -valued truly exchangeable random variables which are *not* i.i.d., that is, the exchangeable  $\sigma$ -algebra is not trivial. This means that the limiting empirical mean turns out to be a *random variable* and this is the driving term due to migration for the local evolution of a site in the McKean-Vlasov limit. Therefore both the random driving term and the non-linearity of the evolution equation come seriously into play. However once we condition on the exchangeable  $\sigma$ -algebra, we then get for the further evolution again a deterministic limiting equation for the empirical measures, namely the McKean-Vlasov equation. The reason for this is the fact that conditioned on the exchangeable  $\sigma$ -algebra we obtain an asymptotically (as  $N \rightarrow \infty$ ) i.i.d. configuration to which the classical convergence theorem applies. Using the Feller property of the system, we get our claim. This leads to the task of identifying an entrance law in terms of a *random initial condition at time  $-\infty$* .

The above discussion shows that we need to introduce the notion of a truly random McKean-Vlasov entrance law from  $-\infty$ .

**Definition 1.9** (Random entrance laws of McKean-Vlasov from  $t = -\infty$ )

We say that the probability measure-valued process  $\{\mathcal{L}(t)\}_{t \in \mathbb{R}}$  is a random solution of the McKean-Vlasov equation (0.32) if

- $\{\mathcal{L}_t : t \in \mathbb{R}\}$  is a.s. a solution to (0.32), that is, for every  $t_0$  the distribution of  $\{\mathcal{L}_t : t \geq t_0\}$  conditioned on  $\mathcal{F}_{t_0} = \sigma\{\mathcal{L}_s : s \leq t_0\}$  is given by  $\delta_{\{\mu_t\}_{t \geq t_0}}$  where  $\mu_t$  is a solution of the McKean-Vlasov equation with  $\mu_{t_0} = \mathcal{L}_{t_0}$ ,
- the time  $t$  marginal distributions of  $\{\mathcal{L}_t : t \in \mathbb{R}\}$  are truly random.  $\square$

We can say the following about the possible random entrance laws.

**Proposition 1.10** (Random entrance laws)

(a) There exists a solution  $(\mathcal{L}_t^{**}(2))_{t \in \mathbb{R}}$  to equation (0.32) satisfying the conditions:

$$(0.50) \quad \begin{aligned} \lim_{t \rightarrow -\infty} \mathcal{L}_t^{**}(2) &= \delta_0, \\ \lim_{t \rightarrow \infty} \mathcal{L}_t^{**}(2) &= \delta_1 \\ \int_{[0,1]} x \mathcal{L}_0^{**}(2, dx) &= \frac{1}{2}. \end{aligned}$$

This solution is called an entrance law from  $-\infty$  with mean  $\frac{1}{2}$  at  $t = 0$ .

(b) We can obtain a solution in (a) such that:

$$(0.51) \quad \exists \alpha \in (0, s) \text{ and } A_0 \in (0, \infty) \text{ such that } \lim_{t \rightarrow -\infty} e^{\alpha|t|} \int_{[0,1]} x \mathcal{L}_t^{**}(2, dx) = A_0.$$

(c) The solution of (0.32) also satisfying (0.51) for prescribed  $A_0$  is unique and if  $A_0 \in (0, \infty)$  then  $\alpha$  is necessarily uniquely determined.

For any deterministic solution

$$(0.52) \quad \{\mathcal{L}_t, t \in \mathbb{R}\}$$

to (0.32) with

$$(0.53) \quad 0 \leq \limsup_{t \rightarrow -\infty} e^{\alpha|t|} \int_{[0,1]} x \mathcal{L}_t(2, dx) < \infty,$$

the limit  $A = \lim_{t \rightarrow -\infty} e^{\alpha|t|} \int_{[0,1]} x \mathcal{L}_t(2, dx)$  exists.

If  $A > 0$ , then  $\{\mathcal{L}_t, t \in \mathbb{R}\}$  is given by a time shift of the then unique  $\{\mathcal{L}_t^{**}, t \in \mathbb{R}\}$  singled out in (0.51), i.e.

$$(0.54) \quad \mathcal{L}_t = \mathcal{L}_{t+\tau}^{**}, \quad \tau = \alpha^{-1} \log \frac{A}{A_0}.$$

For future reference we define  $(\mathcal{L}_t^*)_{t \in \mathbb{R}}$  to be the unique solution satisfying

$$(0.55) \quad \lim_{t \rightarrow -\infty} e^{\alpha|t|} \int_{[0,1]} x \mathcal{L}_t^*(2, dx) = 1 \text{ for some } \alpha \in (0, s).$$

(d) Any random solution  $(\mathcal{L}_t)_{t \in \mathbb{R}}$  to (0.32) such that

$$(0.56) \quad \limsup_{t \rightarrow -\infty} e^{\alpha|t|} E\left[\int_{[0,1]} x \mathcal{L}_t(2, dx)\right] < \infty, \quad \liminf_{t \rightarrow -\infty} e^{\alpha|t|} \left[\int_{[0,1]} x \mathcal{L}_t(2, dx)\right] > 0 \text{ a.s.,}$$

is a random time shift of  $(\mathcal{L}_t^{**})_{t \in \mathbb{R}}$  and of  $(\mathcal{L}_t^*)_{t \in \mathbb{R}}$ .  $\square$

**Example 1** Let  $\mathcal{L}_t^*$  be a solution satisfying (0.36), (0.51) and for a given value of  $A$  let  $\tau$  be a true real-valued random variable. Then  $\{\mathcal{L}_{t-\tau}^*\}_{t \in \mathbb{R}}$  is a truly random solution. This can also be viewed as saying that we have a solution with an exponential growth factor  $A$  which is truly random.

The emergence of the advantageous type and the subsequent evolution to fixation in this type is characterized as follows.

**Proposition 1.11** (Asymptotic macroscopic emergence-fixation process)

(a) For each  $-\infty < t < \infty$  the empirical measures converge weakly to a random measure:

$$(0.57) \quad \mathcal{L}[\{\Xi_N^{\log, \alpha}(t, \ell)\}] \xrightarrow{N \rightarrow \infty} \mathcal{L}[\{\mathcal{L}_t(\ell)\}] = P_t^\ell \in \mathcal{P}(\mathcal{P}([0, 1])), \text{ for } \ell = 1, 2.$$

In addition we have path convergence:

$$(0.58) \quad w - \lim_{N \rightarrow \infty} \mathcal{L}[(\Xi_N^{\log, \alpha}(t))_{t \in \mathbb{R}}] = P \in \mathcal{P}[C((-\infty, \infty), \mathcal{P}(\mathcal{P}(\{0, 1\})))].$$

A realization of  $P$  is denoted  $(\mathcal{L}_t)_{t \in \mathbb{R}}$  respectively its marginal processes  $(\mathcal{L}_t(1))_{t \in \mathbb{R}}, (\mathcal{L}_t(2))_{t \in \mathbb{R}}$ .

(b) The process  $(\mathcal{L}_t)_{t \in \mathbb{R}}$  describes the emergence and fixation dynamics, that is, for  $t \in \mathbb{R}$ , and  $\varepsilon > 0$ ,

$$(0.59) \quad \lim_{t \rightarrow -\infty} \text{Prob}[\mathcal{L}_t(2)((\varepsilon, 1]) > \varepsilon] = 0,$$

$$(0.60) \quad \lim_{t \rightarrow \infty} \text{Prob}[\mathcal{L}_t(2)([1 - \varepsilon, 1]) < 1 - \varepsilon] = 0,$$

with

$$(0.61) \quad \mathcal{L}_t(2)((0, 1)) > 0 \quad , \quad \forall t \in \mathbb{R}, \text{ a.s..}$$

(c) The limiting dynamic in (0.58) is identified as follows:

The probability measure  $P$  in (0.58) is such that the canonical process is a random solution (recall Definition 1.9) and entrance law from time  $-\infty$  to the McKean-Vlasov equation (0.32).

(d) The limiting dynamic in (0.58) satisfies with  $\alpha$  as in (0.39):

$$(0.62) \quad \mathcal{L}[e^{\alpha|t|} \int_{[0,1]} x \mathcal{L}_t(2)(dx)] \Rightarrow \mathcal{L}[*\mathcal{W}] \text{ as } t \rightarrow -\infty,$$

and we explicitly identify the random element generating  $P$  in (0.58), namely  $P$  arises from random shift of a deterministic path:

$$(0.63) \quad P = \mathcal{L}[\tau_* \mathcal{E}^*] \quad , \quad *\mathcal{E} = (\log^* \mathcal{W})/\alpha, \quad \tau_r \text{ is the time-shift of path by } r,$$

where  $\mathcal{L}^*$  is the unique and deterministic entrance law of the McKean-Vlasov equation (0.32) with projection  $\mathcal{L}_t^*(2)$  on the type 2 coordinate satisfying:

$$(0.64) \quad e^{\alpha|t|} \int_{[0,1]} x \mathcal{L}_t^*(2)(dx) \longrightarrow 1, \text{ as } t \rightarrow -\infty.$$

The random variable  $*\mathcal{W}$  satisfies

$$(0.65) \quad 0 < *\mathcal{W} < \infty \text{ a.s., } E[*\mathcal{W}] < \infty, \quad 0 < \text{Var}(*\mathcal{W}) < \infty.$$

(e) We have for  $s_N \rightarrow \infty$  with  $s_N = o(\log N)$  the approximation property for the growth behaviour of the limit dynamic by the finite  $N$  model, namely:

$$(0.66) \quad \mathcal{L}[e^{\alpha s_N} \bar{x}_2^N (\frac{\log N}{\alpha} - s_N)] \xrightarrow{N \rightarrow \infty} \mathcal{L}[*\mathcal{W}]. \quad \square$$

How does this emergence in (0.66) relate to the droplet growth? We have

**Proposition 1.12** (*Microscopic emergence and evolution: droplet formation*)

The total type-2 mass  $\mathfrak{I}_{t_N}^{N,m}([0,1])$  grows at exponential rate  $\alpha$ ,

$$(0.67) \quad \mathcal{L} \left[ \mathfrak{I}_{t_N}^{N,m}([0,1]) e^{-\alpha t_N} \right] \xrightarrow[N \rightarrow \infty]{} \mathcal{L}[\mathcal{W}^*], \quad \text{for } t_N \uparrow \infty \text{ with } t_N - (\alpha^{-1} \log N) \rightarrow -\infty,$$

$$(0.68) \quad \mathcal{L}[*\mathcal{W}] = \mathcal{L}[\mathcal{W}^*]. \quad \square$$

## 2 A logistic branching random walk and its growth

We define here a logistic branching population, take the mean-field limit  $N \rightarrow \infty$ , study the expansion of the droplet of occupied sites, determine the late time window and finally the behaviour in a late time window (i.e. shift of observation time interval and size of space tend to infinity) in four subsections.

### 2.1 The logistic branching particle model

We now consider a particle system on the geographic space  $\{1, \dots, N\}$  and its occupation number configuration with state space

$$(0.69) \quad (\mathbb{N}_0)^{\{1, \dots, N\}}.$$

Here particles

- *migrate* according to a continuous time (rate  $c$ ) random walk with uniform step distribution,
- a particular particle at a site  $i$  *dies* at rate  $d(k-1)$  if we have  $k$  particles at site  $i$ ,
- a particle has *one offspring* at rate  $s$  which is placed at the same site.

This defines uniquely a strong Markov pure jump process on our state space, which we denote by

$$(0.70) \quad (\eta_t^N)_{t \geq 0}.$$

**Remark 5** Note that the mean production rate (mean growth rate) of this model in state  $k$  is

$$(0.71) \quad sk - d(k(k-1)),$$

which is a concave function  $f$  with  $f(0) = 0$ ,  $f(1) = s1$ ,  $f(k) > 0$  for  $k \leq k_0$  and  $f(k) < 0$  for  $k > k_0$ . This production rate can be interpreted as reflecting limited local resources for a population.

**Remark 6** We can view this process as a supercritical branching random walk (supercriticality parameter  $s$ ) with an additional linear death rate  $d(k-1)$  per individual thus inducing an interaction between families. The process is also called a coalescing branching random walk.

Due to the quadratic death rate the population can only expand indefinitely by having individuals move to sites where so far no particles are sitting. When the space is filled the expansion of the population is replaced by an equilibrium situation. How to make this precise?

We want to study this particle system for  $N \rightarrow \infty$  in finite time windows, one early starting at time 0 and the other time windows beginning at a late time when space fills up with particles. Here we start with one particle and determine the late time window by asking when does the population

develop a positive spatial intensity even as  $N \rightarrow \infty$ . Then in particular we focus on the influence of the deathrate  $d$  and the migration rate  $c$  on the speed of spatial spread. The goal then is to establish that the population grows exponentially fast with a rate  $\alpha$  which is positive but strictly less than the birth rate  $s$  as long as we have no collisions.

**Remark 7** *Note that if  $d = 0$ , then in fact we have a supercritical branching process at exponential rate  $s$  and it would take time  $\frac{1}{s} \log N$  to develop positive spatial intensity.*

If we have only one site we have a classical birth and death process, in the spatial model we have a collection of such processes. Since the death rate is zero if we have only one particle at a site, and furthermore because the death rate is quadratic, we have a positive recurrent Markov process on the state space  $\mathbb{N}_0^N$  with a unique equilibrium law denoted:

$$(0.72) \quad \pi^N = \pi_{c,s,d}^N. \text{ Write } \pi_{c,s,d} \text{ for } \pi_{c,s,d}^1.$$

Out of the finite initial state a new site can be occupied and the population can grow till the jumps can only hit already occupied sites and this way a population intensity on the whole space can develop and a local equilibrium forms, resulting in a global equilibrium density.

## 2.2 The early time window as $N \rightarrow \infty$

As  $N \rightarrow \infty$  the geographic space expands to  $\mathbb{N}$  and the migrating particles eventually do not hit occupied sites in a fixed time interval (if we start with finitely many initial particles, the collision-free regime, later when collisions occur sites interact again). More precisely, we want to establish that, as  $N \rightarrow \infty$ , we get as limit dynamic a collection of birth and death processes with emigration at rate  $c$  and immigration at rate  $c$  from a reservoir with the current intensity in the total population. This is carried out as follows.

Consider a branching random walk with birth and death as before but now with geographic space  $\mathbb{N}$ , so that the state space becomes

$$(0.73) \quad (\mathbb{N}_0)^N$$

and migration changes to

- emigration out of any component at rate  $c$  to the unoccupied site of lowest index as long as there is more than one particle
- immigration at rate  $c \cdot \iota$  into every colony, with  $\iota \in [0, \infty)$ .

Here if we start the system in an exchangeable initial state we choose

$$(0.74) \quad \iota = \lim_{N \rightarrow \infty} (N^{-1} \sum_{i=1}^N \eta(i)).$$

Later in larger time scales we will obtain a  $\iota$  which is time-dependent and arises from the law at a tagged site. For  $\iota = 0$  we obtain what we call the *collision-free process*.

The strong Markov process defined by the above McKean-Vlasov dynamic is denoted

$$(0.75) \quad (\eta_t^i)_{t \geq 0} \quad (\text{resp. } (\eta_t)_{t \geq 0} \text{ if } \iota = 0).$$

This process has for every value  $\iota \in [0, \infty)$  a unique equilibrium

$$(0.76) \quad \Pi^\iota = \bigotimes \pi_{c,s,d}^{(\iota)},$$

where  $\pi_{c,s,d}^\iota$  is the single site equilibrium. Let  $r$  be any map which permutes the location such that  $1, 2, \dots, |\{i | \eta_t^N(i) > 0\}|$  are all occupied and acts on paths by achieving the constraint at the final time. We prove

**Proposition 2.1** (*Convergence to  $\iota$ -process, collision-free process*)

*If we start in an i.i.d. distribution with  $E[\eta_t^N(i)] = \iota$ , then*

$$(0.77) \quad \mathcal{L}[(\eta_t^N)_{t \geq 0}] \xrightarrow[N \rightarrow \infty]{} \mathcal{L}[(\eta_t^{(\iota)})_{t \geq 0}].$$

*If we start with one initial particle at site 1 and if  $t_N = o(\log N)$ , then*

$$(0.78) \quad \mathcal{L}[(r \circ \eta_t^N)_{t \geq 0}] \xrightarrow[N \rightarrow \infty]{} \mathcal{L}[(\eta_t)_{t \geq 0}]. \quad \square$$

### 2.3 The droplet expansion and Crump-Mode-Jagers processes

As time gets large we expect the populations of particles to occupy more and more sites (droplet), such that the overall population expands as time grows, i.e. we have a growing *droplet of occupied sites*. This droplet growth is expected to be exponential and as time grows to become (at least the further evolution) more and more deterministic due to a law of large numbers effect. Here we have to distinguish a time window, which is late but where particles essentially always move to new unoccupied sites if they migrate and a later phase where spatial intensity builds up and collisions play a role. This subsection handles the first regime.

If we establish an exponential growth behaviour we would be able to determine the position of the late time window where the population density becomes positive as time and  $N$  tend to infinity. How can we make all this rigorous?

To analyse this time window an important concept is that of a CMJ-process (Crump-Mode-Jagers process) which allows us to describe the number of occupied sites in the process  $(\eta_t)_{t \geq 0}$  starting from finitely many particles occupying all sites  $1, \dots, k$  with  $k \geq 1$ . Let

$$(0.79) \quad K_t = \#\{i \in \mathbb{N} | \eta_t(i) > 0\},$$

$$(0.80) \quad \zeta_t = \{\zeta_t(i), \quad i = 1, \dots, K_t\} \quad , \quad \zeta_t(i) = \eta_t(i), \quad i = 1, \dots, K_t.$$

We will find that  $K, \zeta$  are processes which have the structure of a CMJ-process that is the process of *occupied sites* is a type of generalised branching process. We begin by recalling this concept.

#### 1. Crump-Mode-Jagers process

The CMJ-process models individuals in a branching population whose dynamics is as follows. Individuals can die or give birth to new individuals based on the following ingredients:

- individuals have a lifetime (possibly infinite),
- for each individual an independent realization of a point process  $\xi(t)$  starting at the birth time specifying the times at which the individual gives birth to new individuals,
- different individuals act independently,
- the process of birth times is not concentrated on a lattice.

The process might be growing exponentially and then we want to determine its exponential growth rate. The corresponding *Malthusian parameter*,  $\alpha > 0$  is obtained as the unique solution of

$$(0.81) \quad \int_0^\infty e^{-\alpha t} \mu(dt) = 1 \text{ where } \mu([0, t]) = E[\xi([0, t])],$$

with

$$(0.82) \quad \xi(t) \text{ counting the number of births of a single individual up to time } t,$$

(see for example [J92], [N] equation (1.4)).

If we know the Malthusian parameter, we need to know that it is actually equal to the almost sure growth rate of the population. It is known for a CMJ-process  $(K_t)_{t \geq 0}$  that (Proposition 1.1 and Theorem 5.4 in [N]) the following basic growth theorem holds. If

$$(0.83) \quad E[X \log(X \vee 1)] < \infty, \quad \text{where } X = \int_0^\infty e^{-\alpha t} d\xi(t),$$

then

$$(0.84) \quad \lim_{t \rightarrow \infty} \frac{K_t}{e^{\alpha t}} = W, \text{ a.s. and in } L_1,$$

where  $W$  is a random variable which has two important properties, namely

$$(0.85) \quad W > 0, \text{ a.s. and } E[W] < \infty.$$

The empirical distribution of individuals of a certain age in the population converges as  $t \rightarrow \infty$  to a *stable age distribution*

$$(0.86) \quad \mathcal{U}(\infty, du) \text{ on } [0, \infty),$$

according to Corollary 6.4 in [N], if condition 6.1 therein holds. The condition 6.1 in [N] or (3.1) in [JN] requires that (with  $\mu$  as in (0.81)):

$$(0.87) \quad \int_0^\infty e^{-\beta t} \mu(dt) < \infty \quad \text{for some } \beta < \alpha.$$

## 2. Application of the CMJ-theory to $(K_t, \zeta_t)$

The  $(\zeta_t)_{t \geq 0}$  we have introduced is a CMJ where individuals are the occupied sites and satisfying all the conditions posed above. In addition we have more structure, namely the birth process is determined from an *internal state* of the individual (here a site) which follows a Markovian evolution (here our  $(\zeta_t(i))_{t \geq 0}$ ). This allows to obtain some stronger statements as follows.

Define

$$(0.88) \quad (\zeta_0(t, i))_{t \geq 0}, \text{ as the process } (\zeta_t(i))_{t \geq 0} \text{ if } i \text{ gets occupied at time } 0.$$

In our case we then have

$$(0.89) \quad \mu([0, t]) = c \int_0^t E[\zeta_0(s) 1_{(\zeta_0(s) \geq 2)}] ds.$$

Define the random measure

$$(0.90) \quad \mathcal{U}(t, du, j) = \#\{\text{sites of size } j \text{ with birth time } t - du\} K_t^{-1}.$$

It follows that the random measure  $\mathcal{U}(t, \cdot, \cdot)$  converges to a *deterministic* object, the *stable age and size* distribution, i.e.

$$(0.91) \quad \mathcal{U}(t, \cdot, \cdot) \implies \mathcal{U}(\infty, \cdot, \cdot), \text{ as } t \rightarrow \infty \text{ in law, } \mathcal{U}(\infty, \cdot, \mathbb{N}) = \mathcal{U}(\infty, \cdot) \text{ from (0.86).}$$

We can obtain from this the following representation of the Malthusian parameter  $\alpha$ .

Given site  $i$  let  $\tau_i \geq 0$  denote the time at which a migrant (or initial particle) first occupies it. Noting that we can verify Condition 5.1 in [N] we have that

$$(0.92) \quad \lim_{t \rightarrow \infty} \frac{1}{K_t} \sum_{i=1}^{K_t} \zeta_{\tau_i}(t - \tau_i) = \int_0^\infty E[\zeta_0(u)] \mathcal{U}(\infty, du) = B \text{ (a constant), a.s.,}$$

by Corollary 5.5 of [N]. The constant  $B$  in (0.92) is in our case given by the average number of particles per occupied site and the growth rate  $\alpha$  arises from this quantity neglecting single occupation. Namely define

$$(0.93) \quad \alpha = c \sum_{j=2}^{\infty} j \mathcal{U}(\infty, [0, \infty), j) < \infty, \quad \gamma = c \mathcal{U}(\infty, [0, \infty), 1).$$

Then the mean occupation number of an occupied site is given by

$$(0.94) \quad B = \frac{\alpha + \gamma}{c} > 0.$$

Furthermore the average birth rate of new sites (by arrival of a migrant at an unoccupied site) at time  $t$  (in the process in the McKean-Vlasov dual) is equal to

$$(0.95) \quad \alpha = c B - \gamma.$$

Here a remarkable point is the relation between  $\alpha$  and  $s$ . Recall  $s$  is the parameter of supercriticality in the branching part of the internal state dynamics. The action of the quadratic death part and the role of migration lead to a number  $\alpha$  with

$$(0.96) \quad 0 < \alpha < s,$$

since the fraction of the supercritical branching process with supercriticality parameter  $s$  which die by the quadratic death rate is positive.

## 2.4 Time point of emergence as $N \rightarrow \infty$

If we take the collision-free model  $(\eta_t)_{t \geq 0}$  and we observe at time  $T_N(t) = \alpha^{-1} \log N + t$  the number of individuals or the number of occupied sites, both normalized by  $N$ , then these quantities satisfy (recall (0.94), (0.84))

$$(0.97) \quad \left( \frac{1}{N} \sum_{i=1}^{K_{T_N(t)}} \eta_{T_N(t)}(i) \right) \xrightarrow[N \rightarrow \infty]{} B e^{\alpha(t + \alpha^{-1} \log W)}, \quad (K_{T_N(t)}/N)_{t \in \mathbb{R}} \xrightarrow[N \rightarrow \infty]{} (e^{\alpha(t + \alpha^{-1} \log W)})_{t \in \mathbb{R}},$$

with  $0 < W < \infty$  a.s. and  $\text{Var}(W) > 0$ . Hence a positive intensity develops:

$$(0.98) \quad \left( \frac{1}{K_{T_N(t)}} \sum_{i=1}^{K_{T_N(t)}} \eta_{T_N(t)}(i) \right) \xrightarrow[N \rightarrow \infty]{} B, \quad \forall t \in \mathbb{R}.$$

In particular in this time window  $\eta^N$  and  $\eta$  differ significantly, but one can show that still:

$$(0.99) \quad \mathcal{L}[(\{r \circ \eta_{T_N+t}^N(1), \dots, (r \circ \eta_{T_N+t}^N(k))\}_{t \geq 0}] \implies \mathcal{L}[(\eta_t(1), \dots, \eta_t(k))_{t \geq 0}], \text{ as } N \rightarrow \infty,$$

provided  $T_N - \alpha^{-1} \log N \rightarrow -\infty$  as  $N \rightarrow \infty$ . In fact even though the CMJ-approximation breaks down at times  $\alpha \log N + t$  we can still prove emergence occurs at time  $\alpha^{-1} \log N$ , since  $\eta^N$  develops a positive intensity meaning the total population is comparable to  $N$ , which as  $t \rightarrow -\infty$  is asymptotically equivalent to the r.h.s. of (0.97). Indeed time  $\alpha^{-1} \log N$  separates the collision-free droplet growth from the emergence.

**Proposition 2.2** (*Emergence of positive intensity*)

We have for  $N \rightarrow \infty$  and  $\nu = \nu((t_N)_{N \in \mathbb{N}})$ :

$$(0.100) \quad \mathcal{L}[N^{-1} \sum_{i=1}^N \eta_{t_N}^N(i)] \xrightarrow[t \rightarrow \infty]{} \begin{cases} \delta_0, & t_N - \alpha^{-1} \log N \rightarrow -\infty \\ \nu, \nu((0, \infty)) = 1, & \lim_{N \rightarrow \infty} (t_N - \alpha^{-1} \log N) = t > -\infty. \end{cases} \quad \square$$

## 2.5 The late time window as $N \rightarrow \infty$

To treat the time window  $\alpha^{-1} \log N + t$  and to obtain the limiting emergence-equilibration dynamics based on *random entrance laws* of the *McKean-Vlasov equation*, we need some ingredients.

We consider the number of sites occupied at time  $t$  denoted  $K_t^N$  and the corresponding measure-valued process on  $[0, \infty) \times \mathbb{N}_0$  giving the unnormalized number of sites of a certain age  $u$  in  $[a, b]$  and occupation size  $j$ :

$$(0.101) \quad \Psi^N(t, [a, b], j) = \int_{(t-b)}^{(t-a)} 1_{(K_u^N > K_{u-}^N)} 1_{(\zeta_u^N(t)=j)} dK_u^N,$$

where  $\zeta_u^N(t)$  denotes the occupation number at time  $t$  of the site born at time  $u$ , that is, a site first occupied the last time at time  $u$ , which is therefore at time  $t$  exactly of age  $t - u$ .

The *normalized empirical age and size distribution* among the occupied sites is defined as:

$$(0.102) \quad U^N(t, [a, b], j) = \frac{1}{K_t^N} \Psi^N(t, [a, b], j), \quad t \geq 0, j \in \{1, 2, 3, \dots\}.$$

Denote now for convenience the number of sites:

$$(0.103) \quad u^N(t) := K_t^N.$$

We have obtained with (0.102), (0.103) a pair which is  $\mathbb{N} \times \mathcal{P}([0, \infty) \times \mathbb{N})$ -valued and which describes our particle system completely provided if we consider individuals and sites as exchangeable labels. This pair is denoted

$$(0.104) \quad (u^N(t), U^N(t, \cdot, \cdot))_{t \geq 0}.$$

In the interval  $\alpha^{-1}[\log N - \log \log N, \log N + T]$  the process  $(u^N(t))_{t \geq 0}$  increases by one respectively decreases by one at rates

$$(0.105) \quad \alpha_N(t)(1 - \frac{u^N(t)}{N})u^N(t), \text{ respectively } \gamma_N(t)\frac{(u^N(t))^2}{N},$$

where  $\alpha_N(t), \gamma_N(t)$  are defined:

$$(0.106) \quad \alpha_N(t) = c \int_0^t \sum_{j=2}^{\infty} j U^N(t, ds, j) ds, \quad \gamma_N(t) = c \int_0^t U^N(t, ds, 1).$$

The above rates of change of  $U^N(t, \cdot, \cdot)$  follow directly from the dynamics of the particle system  $\eta^N$ .

Our goal is now to study the behaviour of  $(u^N, U^N)$  at times  $\alpha^{-1} \log N + t$  and to show that this follows a limiting fixation dynamics. We start the system with  $k$  particles at  $\ell$  distinct sites and write  $k, \ell$  as superscript. We need the time-shifted quantities:

$$(0.107) \quad \tilde{u}^{N,k,\ell}(t) = u^{N,k,\ell}((\frac{\log N}{\alpha} + t) \vee 0), \quad t \in (-\infty, T], \quad \tilde{u}^{N,k,\ell}(-\frac{\log N}{\alpha}) = \ell$$

$$(0.108) \quad \tilde{U}^{N,k,\ell}(t) = U^{N,k,\ell}((\frac{\log N}{\alpha} + t) \vee 0), \quad t \in (-\infty, T], \quad \tilde{U}^{N,k,\ell}(-\frac{\log N}{\alpha}) = \delta_{(k,0)}.$$

**Proposition 2.3** (*Convergence to a colonization-equilibration dynamic in the  $N \rightarrow \infty$  limit*)

Assume that for some  $t_0 \in \mathbb{R}$  as  $N \rightarrow \infty$ ,  $(\frac{1}{N} \tilde{u}^{N,k,\ell}(t_0), \tilde{U}^{N,k,\ell}(t_0))$  converges in law to the pair  $(u(t_0), U(t_0))$  automatically contained in  $[0, \infty) \times L_1(\mathbb{N}, \nu)$ .

Then as  $N \rightarrow \infty$

$$(0.109) \quad \mathcal{L} \left[ \left( \frac{1}{N} \tilde{u}^{N,k,\ell}(t), \tilde{U}^{N,k,\ell}(t, \cdot, \cdot) \right)_{t \geq t_0} \right] \Rightarrow \mathcal{L} [(u^{k,\ell}(t), U^{k,\ell}(t, \cdot, \cdot))_{t \geq t_0}],$$

in law on pathspace, where the r.h.s. is supported on the solution of the nonlinear system (0.111) and (0.112) corresponding to the initial state  $(u(t_0), U(t_0))$ . (Note that the mechanism of the limit dynamics does not depend on  $k$  or  $\ell$ , but the state at  $t_0$  will.)  $\square$

We obtain the limiting system  $(u, U)$  as follows. We specify the pair

$$(0.110) \quad (u, U) = (u(t), U(t))_{t \in \mathbb{R}}, \quad \text{with } (u(t), U(t)) \in \mathbb{R}^+ \times \mathcal{M}_1(\mathbb{R}^+ \times \mathbb{N}),$$

by the (coupled) system of nonlinear *forward* evolution equations:

$$(0.111) \quad \frac{du(t)}{dt} = \alpha(t)(1 - u(t))u(t) - \gamma(t)u^2(t),$$

$$(0.112) \quad \begin{aligned} & \frac{\partial U(t, dv, j)}{\partial t} \\ &= - \frac{\partial U(t, dv, j)}{\partial v} \\ & \quad + s(j-1)1_{j \neq 1} U(t, dv, j-1) - sj U(t, dv, j) \\ & \quad + \frac{d}{2}(j+1)j U(t, dv, j+1) - \frac{d}{2}j(j-1)1_{j \neq 1} U(t, dv, j) \\ & \quad + c(j+1)U(t, dv, j+1) - cj U(t, dv, j)1_{j \neq 1} \\ & \quad - cu(t)U(t, dv, 1)1_{j=1} \\ & \quad + u(t)(\alpha(t) + \gamma(t))[1_{j \neq 1} U(t, dv, j-1) - U(t, dv, j)] \\ & \quad + ((1 - u(t))\alpha(t))1_{j=1} \cdot \delta_0(dv) \\ & \quad - \left( \alpha(t)(1 - u(t)) - \gamma(t)u(t) \right) \cdot U(t, dv, j). \end{aligned}$$

We have to constrain the state space to guarantee the r.h.s. above is well-defined. Set therefore  $\nu$  to be the measure on  $\mathbb{N}$  given by

$$(0.113) \quad \nu(j) = 1 + j^2$$

and consider  $\mathbb{R} \otimes L^1(\nu, \mathbb{N})$  as a basic space for the analysis. Then the equations (0.111), (0.112) have the following properties.

**Proposition 2.4** (*Uniqueness of the pair  $(u, U)$* )

(a) *The pair of equations (0.111) - (0.112), given an initial state from  $\mathbb{R}^+ \times \mathcal{M}_1(\mathbb{R}^+ \times \mathbb{N})$  satisfying*

$$(0.114) \quad (u(0), U(0, \cdot, \cdot)) \in \mathbb{R} \otimes L^1(\mathbb{N}, \nu)$$

*at time  $t_0$ , has a unique solution  $(u(t), U(t))_{t \geq t_0}$  with values in  $\mathbb{R}^+ \otimes L^1_+(\mathbb{N}, \nu)$ , which satisfies  $u \geq 0$  and  $U(t, \mathbb{R}^+ \times \mathbb{N}) \equiv 1$ .*

(b) *There exists a solution  $(u, U)$  with time parameter  $t \in \mathbb{R}$  for every  $A \in (0, \infty)$  with values in  $\mathbb{R} \otimes L^1(\mathbb{N}, \nu)$ , such that*

$$(0.115) \quad u(t)e^{-\alpha t} \rightarrow A \text{ as } t \rightarrow -\infty,$$

$$(0.116) \quad U(t) \xrightarrow[t \rightarrow -\infty]{} \mathcal{U}(\infty).$$

*Here  $\mathcal{U}(\infty)$  is the stable age and size distribution of the CMJ-process corresponding to the particle process  $(K_t, \zeta_t)_{t \geq 0}$  given by the McKean-Vlasov dual process  $\eta$ , as defined in (0.80).*

(c) *Given any solution  $(u, U)$  of equations (0.111) - (0.112) for  $t \in \mathbb{R}$  with values in the space  $\mathbb{R} \otimes L^1(\mathbb{N}, \nu)$  satisfying*

$$(0.117) \quad u(t) \geq 0, \quad \limsup_{t \rightarrow -\infty} e^{-\alpha t} u(t) < \infty,$$

*we then have for  $u$*

$$(0.118) \quad A = \lim_{t \rightarrow -\infty} e^{-\alpha t} u(t)$$

*exists and the solution satisfying this for given  $A$  is unique. Furthermore  $U$  satisfies*

$$(0.119) \quad U(t) \implies \mathcal{U}(\infty) \text{ as } t \rightarrow -\infty. \quad \square$$

**Remark 8** *Potential limits arising from  $(u^N, U^N)$  do satisfy equation (0.117).*

**Remark 9** *Note that looking at the form of the equation we see that a solution indexed by  $\mathbb{R}$  remains a solution if we make a time shift. This corresponds to the different possible values for the growth constant  $A$  in (0.115). In particular the entrance law from 0 at time  $-\infty$  is unique up to the time shift.*

We can now identify the behaviour of  $(u^N, U^N)$  for  $N \rightarrow \infty$  in terms of the early growth behaviour of the droplet of colonized sites as follows.

**Proposition 2.5** (*Identification of colonization-equilibrium dynamics*)

*The limits  $(u^{k,\ell}(t), U^{k,\ell}(t, \cdot, \cdot))_{t \geq t_0}$ , in (0.109) can be represented as the unique solution of the nonlinear system (0.111) and (0.112) satisfying*

$$(0.120) \quad \lim_{t \rightarrow -\infty} e^{-\alpha t} u^{k,\ell}(t) = W^{k,\ell}, \quad \lim_{t \rightarrow -\infty} U^{k,\ell}(t) = \mathcal{U}(\infty),$$

*with  $W^{k,\ell}$  having the law of the random variable appearing as the scaling (by  $e^{-\alpha t}$ ) limit  $t \rightarrow \infty$  of the CMJ-process  $K_t^{k,\ell}$  started with  $k$  particles at each of  $\ell$  sites.  $\square$*

We can now ask, what happens if we consider times  $\alpha^{-1} \log N + t_N$  with  $t_N \rightarrow \infty$ . Then we reach a global stable state. Let  $\tilde{\Pi}_{c,d,s}^{\iota^*} \Pi_{c,d,s}^{\iota^*}$  conditioned to be strictly positive.

**Proposition 2.6** (*Equilibrium population*)

We have

$$(0.121) \quad N^{-1} u^N(\alpha^{-1} \log N + t_N) \xrightarrow[N \rightarrow \infty]{} \iota^* \quad , \quad U^N(\alpha^{-1} \log N + t_N) \xRightarrow[N \rightarrow \infty]{} \tilde{\Pi}_{c,d,s}^{\iota^*},$$

where  $\iota^*$  satisfies the selfconsistency relation:

$$(0.122) \quad \sum_{k=1}^{\infty} k \pi_{c,d,s}^{(\iota)}(\{k\}) = \iota. \quad \square$$

### 3 The duality relation

In this section we relate the processes from section 1 and 2 with each other by duality and we discuss the extension of the duality to more than two types.

#### 3.1 A classical duality formula

The key tool in relating the two processes we have introduced is duality. Recall the classical relation between a single Fisher-Wright diffusion and the Kingman coalescent.

Consider  $(X_t)_{t \geq 0}$  solving

$$(0.123) \quad dX_t = \sqrt{d \cdot X_t(1 - X_t)} dW_t$$

and  $(D_t)_{t \geq 0}$  being the  $\mathbb{N}$ -valued death process

$$(0.124) \quad n \rightarrow n - 1 \text{ at rate } d \cdot \binom{n}{2}.$$

Then a generator calculation shows (we explain more on the background below):

$$(0.125) \quad E_{X_0}[(X_t)^k] = E_k[X_0^{D_t}].$$

The analogous relation can be formulated for our mean-field spatial model including mutation and selection. Define for the process starting with  $k$ -particles at each of  $\ell$  sites:

$$(0.126) \quad \Pi_t^{N,k,\ell} = u^N(t) \sum_{j=1}^{\infty} j U^N(t, \mathbb{R}^+, j),$$

where  $(u^N(t), U^N(t, \mathbb{R}^+, \mathbb{N}))$  are given by (0.104). Then we get by a generator calculation the formula:

$$(0.127) \quad E[x_1^N(i, t)] = E[\exp(-\frac{m}{N} \int_0^t \Pi_u^{N,1,1} du)], \quad i \in \{1, \dots, N\}.$$

Hence if we start initially with  $x_1^N(i, 0) = 1; i = 1, \dots, N$  we see that in order to observe a mean which is less than one we need an occupation measure of the population from the branching coalescing random walk which is of order  $N$ . Due to the exponential growth this amounts to  $\Pi^{N,1,1}$  to grow up to

order  $N$ . Since we proved the latter behaves at times  $\alpha^{-1} \log N + t$  for very negative  $t$  approximately like

$$(0.128) \quad W \exp(\alpha(\alpha^{-1} \log N + t)) = e^{\alpha t} \cdot WN,$$

the advantageous type emerges since  $E[x_1^N(1, \alpha^{-1} \log N + t)]$  is as  $N \rightarrow \infty$  for  $t \in \mathbb{R}$  strictly between 0 and 1. By the analysis of moments we actually can prove the results on the Fisher-Wright diffusion model stated in section 1 from the results of the coalescing particles model stated in section 2. In section 7 of [DGsel] methods are developed to turn this idea into rigorous mathematics.

## 3.2 The genealogy and duality

The formula (0.125) can be understood on a deeper level, since the dual process can be interpreted in terms of the genealogy of the Fisher-Wright diffusion model. This will also exhibit the role of selection a bit better.

For that purpose the Kingman coalescent has to be viewed as a partition-valued process. This means its states are the partitions of the set  $\{1, \dots, k\}$  starting in  $\{\{1\}, \dots, \{k\}\}$  where partition elements coalesce at rate  $d$  independent of each other (and in the spatial case perform continuous time random walks at rate  $c$ ). If we consider a Fisher-Wright diffusion it can be viewed as the limit of the Moran model taking the population size to infinity. Pick then from the population at time  $t$  exactly  $k$  individuals and look at their genealogy. This genealogy has the same law as the genealogy of the Kingman coalescent with the genealogical distance between two individuals defined to be the first time they are in the same partition element. Given this genealogy we can calculate the probability, that all individuals have the same type, one, which is  $x^k$  if  $x$  is the current (time  $t$ ) frequency of type one, in terms of the Kingman coalescent getting the duality relation (0.125). See [GPWmetric], [GPWmp] for more details on the genealogical processes.

If we include selection note that if we follow the tagged sample from the population back one of the individuals might interact with the rest of the population (note now individuals under selection and mutation are *not* anymore exchangeable) by a selection event. What results from this event however now depends on the current types of the two involved individuals. Therefore we have to also follow the other individual further back. This means we expect that each time a selection event occurs our tagged sample has to be enriched by a further particle. This is reflected in the birth of new individuals in the dual particle model.

In order to handle multiple types and mutation the point now is that the dual process has to be complemented by a function-valued part. The basic idea behind this is explained in the next subsection.

## 3.3 The dual for general type space

The picture from above for two types is more subtle, if we consider a multitype situation with more than 2 types. The basic new ideas for this purpose in [DGsel] we sketch next.

### 3.3.1 A multitype model

The process considered in section 1 can be defined for general type space  $\mathbb{I}$  (a subset of  $[0, 1]$ ) as  $(\mathcal{P}(\mathbb{I}))^S$ -valued process ( $S$  = a finite or countable geographic space) and is called the interacting Fleming-Viot process with selection and mutation, see [DG99], (which becomes a multitype Fisher-Wright diffusion in the case of finitely many types and the model of section 1 for two types). Then

types have a fitness given by a function and mutation occurs via a jump kernel which are denoted respectively by

$$(0.129) \quad \chi : \mathbb{I} \longrightarrow \mathbb{R}^+, \quad 0 \leq \chi \leq 1, \quad M(x, dy) \text{ a } \mathbb{I} \times \mathbb{I}\text{-probability transition kernel.}$$

The generator of the nonspatial Fleming-Viot process acts on monomials of order  $n$  with test function  $f \in C_b(\mathbb{I})$

$$(0.130) \quad F(x) = \int f(u_1, \dots, u_n) x(du_1) \cdots x(du_n), \quad x \in \mathcal{P}(\mathbb{I}),$$

as follows, with setting  $Q_x(du, dv) = x(du)\delta_u(dv) - x(u)x(dv)$ :

$$(0.131) \quad (GF)(x) = s \int_{\mathbb{I}} \left\{ \frac{\partial F(x)}{\partial x}(u) \left( \chi(u) - \int_{\mathbb{I}} \chi(w) x(dw) \right) \right\} x(du) \\ + m \int_{\mathbb{I}} \left\{ \int_{\mathbb{I}} \frac{\partial F(x)}{\partial x}(v) M(u, dv) - \frac{\partial F(x)}{\partial x}(u) \right\} x(du) \\ + d \int_{\mathbb{I}} \int_{\mathbb{I}} \frac{\partial^2 F(x)}{\partial x \partial x}(u, v) Q_x(du, dv) \Bigg], \quad x \in \mathcal{P}(\mathbb{I}).$$

In the spatial case a corresponding drift term from migration appears as well:

$$(0.132) \quad \sum_{i,j \in S} a(i, j) \int \left( \frac{\partial F(x)}{\partial x_j}(u) - \frac{\partial F(x)}{\partial x_i}(u) \right) x_i(du).$$

In [DK] a dual for a Fleming-Viot process with mutation and selection is introduced in order to show that the process is well-defined by its martingale problem. In [DGsel] a new dual was developed which makes possible the study of the long-time behavior and the genealogy of the system. This we explain now. In order to introduce the main ideas we first consider the case with no mutation and the special case  $N = 1$  and then the general case.

### 3.3.2 The dual with selection

Let now the mutation rate be zero and let  $|S| = 1$ , so that the state space is  $\mathcal{P}(\mathbb{I})$  and we only have resampling and selection. Consider the class of functions

$$(0.133) \quad F((n, f), x) := \left[ \int_{\mathbb{I}} \cdots \int_{\mathbb{I}} f(u_1, \dots, u_n) x(du_1) \cdots x(du_n) \right],$$

for all  $n \in \mathbb{N}$ ,  $f \in L_\infty((\mathbb{I})^n, \mathbb{R})$  and  $x \in \mathcal{P}(\mathbb{I})$ . Note that given a random probability measure  $X$  on  $\mathcal{P}(\mathbb{I})$ , the collection

$$(0.134) \quad \{E[F((n, f), X)], n \in \mathbb{N}, f \in L_\infty((\mathbb{I})^n, \mathbb{R})\}$$

uniquely characterizes the probability law of  $X$ .

The class given above contains the functions which we will use for our dual representations. In fact it suffices to take smaller, more convenient sets of test functions  $f$ :

$$(0.135) \quad f(u_1, \dots, u_n) = \prod_{i=1}^n f_i(u_i), \quad f_i \in L_\infty(\mathbb{I}).$$

If we consider the case when  $\mathbb{I}$  is finite, it would even suffice to take functions

$$(0.136) \quad f_j(u) = 1_j(u) \text{ or } f_j(u) = 1_{A_j}(u),$$

where  $1_j$  is the indicator function of  $j \in \mathbb{I}$ .

The *function-valued dual processes*  $(\eta_t, \mathcal{F}_t)_{t \geq 0}$  and  $(\eta_t, \mathcal{F}_t^+)_{t \geq 0}$  are constructed from the following four ingredients:

- $N_t$  the number of *individuals* present in the dual process which is a non-decreasing  $\mathbb{N}$ -valued process with  $N_0 = n$ , the number of initially tagged individuals, and  $N_t \geq n$ ,
- $\zeta_t = \{1, \dots, N_t\}$  is an *ordered particle system*,
- $\pi_t$ : is a *partition*  $(\pi_t^1, \dots, \pi_t^{|\pi_t|})$  of  $\zeta_t$ , i.e. an ordered family of subsets, where the *index* of a partition element is the smallest element of the partition element,
- $\mathcal{F}_t$  is for given states of  $\pi_t, \zeta_t, N_t$  a function in  $L_\infty(\mathbb{I}^{|\pi_t|})$  which is obtained from a function in  $L_\infty(\mathbb{I}^{N_t})$  by setting variables equal which are corresponding to one and the same partition element and  $\mathcal{F}_t$  changes further driven selection (see below).

**Definition 3.1** (*Evolution of  $(\eta, \mathcal{F})$  and  $(\eta, \mathcal{F}^+)$* )

(a) The process  $\eta$  is driven by coalescence at rate  $d$  of every pair of partition elements and by the birth of a new individual at rate  $s$ , which forms its own partition element.

(b) Conditioned on the process  $\eta$  the evolution of  $\mathcal{F}$  is as follows.

- *The coalescence mechanism: If a coalescence of two partition elements occurs, then the corresponding variables of  $\mathcal{F}_t$  are set equal to the variable indexing the partition element, i.e. for  $\mathcal{F}_{t-} = g$  we have the transition (here  $\widehat{u}_j$  denotes an omitted variable)*

$$(0.137) \quad g(u_1, \dots, u_i, \dots, u_j, \dots, u_m) \longrightarrow \widehat{g}(u_1, \dots, \widehat{u}_j, \dots, u_m) \\ = g(u_1, \dots, u_i, \dots, u_{j-1}, u_i, u_{j+1}, \dots, u_m),$$

so that the function changes from an element of  $L_\infty(\mathbb{I}^m)$  to one of  $L_\infty(\mathbb{I}^{m-1})$ .

- *The selection mechanisms:*

- *Feynman-Kac. For  $\mathcal{F}_t$ , if a birth occurs in the process  $(\zeta_s)$  due to the partition element to which the element  $i$  of the basic set belongs, then for  $\mathcal{F}_{t-} = g$  the following transition occurs from an element in  $L_\infty((\mathbb{I})^m)$  to elements in  $L_\infty((\mathbb{I})^{m+1})$ :*

$$(0.138) \quad g(u_1, \dots, u_m) \longrightarrow \chi(u_i)g(u_1, \dots, u_m) - \chi(u_{m+1})g(u_1, \dots, u_m).$$

– Non-negative. For  $\mathcal{F}_t^+$  the transition (0.138) is replaced by (provided that  $\chi$  satisfies  $0 \leq \chi \leq 1$ ):

$$(0.139) \quad g(u_1, \dots, u_m) \longrightarrow \hat{g}(u_1, \dots, u_{m+1}) = (\chi(u_i) + (1 - \chi(u_{m+1})))g(u_1, \dots, u_m). \quad \square$$

Now we can obtain two different duality relations, the first below working in all cases and a second below working in a large subclass of models.

**Proposition 3.2** *(Duality relation - signed with Feynman-Kac dual)*

Let  $(X_t)_{t \geq 0}$  be a solution of the Fisher-Wright martingale with finite type space  $\mathbb{I}$ , fitness function  $\chi$  and selection rate  $s$  with  $X_0 = x \in \mathcal{P}(\mathbb{I})$ . Let  $\mathcal{F}_0 = f \in L_\infty((\mathbb{I})^n)$  for some  $n \in \mathbb{N}$ .

Assume that  $t_0$  is such that:

$$(0.140) \quad E \left( \exp \left( s \int_0^{t_0} |\pi_r| dr \right) \right) < \infty.$$

Then for  $0 \leq t \leq t_0$ ,  $(\eta_t, \mathcal{F}_t)$  is the Feynman-Kac dual of  $(X_t)$ , that is:

$$(0.141) \quad E[F((\eta_0, f), X_t)] = E_{(\eta_0, \mathcal{F}_0)} \left\{ \left[ \exp \left( s \int_0^t |\pi_r| dr \right) \cdot \left[ \int_{\mathbb{I}} \dots \int_{\mathbb{I}} \mathcal{F}_t(u_1, \dots, u_{|\pi_t|}) x(du_1) \dots x(du_{|\pi_t|}) \right] \right] \right\},$$

where the initial state  $(\eta_0, \mathcal{F}_0)$  is for  $n \in \mathbb{N}$  chosen given by

$$(0.142) \quad \begin{aligned} \pi_0 &= [(\{1\}, \{2\}, \dots, \{n\})], \\ \mathcal{F}_0 &= f \in C_b(\mathbb{I}^n). \quad \square \end{aligned}$$

**Remark 10** In [DG99] it was shown that there exists  $t_0 > 0$  for which (0.140) is satisfied.

The disadvantage of the dual above is the exponential term together with the signed function. This involves the interplay of a cancelation effect and the exponential growth factor which is often hard to analyse as  $t \rightarrow \infty$ . The key observation is that if the fitness function  $\chi$  is a bounded function then we can obtain the following duality relation that does *not* involve a Feynman-Kac factor and preserves the positivity of functions:

**Proposition 3.3** *(Duality relation - non-negative)*

With the notation and assumptions as in Proposition 3.2 (except with (0.138) replaced by (0.139)) we get for  $\chi$  with

$$(0.143) \quad 0 \leq \chi \leq 1$$

that for all  $t \in [0, \infty)$  we have:

$$(0.144) \quad E[F((\eta_0, f), X_t)] = E_{(\eta_0, \mathcal{F}_0^+)} \left[ \int_{\mathbb{I}} \dots \int_{\mathbb{I}} \mathcal{F}_t^+(u_1, \dots, u_{|\pi_t|}) x_1(du_1) \dots x_{|\pi_t|}(du_{|\pi_t|}) \right].$$

Moreover,  $\mathcal{F}_t^+$  is always non-negative if  $\mathcal{F}_0^+$  is.  $\square$

### 3.3.3 The dual with migration, selection and mutation

We now consider the case of (0.3), (0.4) including selection and migration but for the moment setting  $m = 0$ . The partition elements of the dual now have *locations* given by

$$(0.145) \quad \xi_t : \pi_t \longrightarrow \Omega_N^{|\pi_t|}.$$

The corresponding additional *dual migration* dynamics is as follows. At rate  $c$  each particle can jump from its current location to a randomly chosen point in  $\{1, \dots, N\}$ . In the limiting case ( $N \rightarrow \infty$ ) the particle always migrates to an empty site which for convenience we can take to be the smallest unoccupied site  $n \in \mathbb{N}$ . This then results in precisely the logistic branching particle model respectively the Crump-Mode-Jagers process described in section 2.

The duality relation is now given by

$$(0.146) \quad E[F((\eta_0, f), X_t)] = E_{(\eta_0, \mathcal{F}_0^+)} \left[ \int_{\mathbb{I}} \cdots \int_{\mathbb{I}} \mathcal{F}_t^+(u_1, \dots, u_{|\pi_t|}) x_{\xi_t(1)}(du_1) \cdots x_{\xi_t(|\pi_t|)}(du_{|\pi_t|}) \right],$$

where  $X_0 = (x_1, \dots, x_n)$ ,  $x_i \in \mathcal{P}(\mathbb{I})$ ,  $i = 1, \dots, N$ ,  $\eta_0 = (\zeta_0, \pi_0, \xi_0)$ .

The mutation can now be incorporated by adding a corresponding transition of  $\mathcal{F}$ , at rate  $m$  for every variable the operation acting on  $g \in (L^\infty(\mathbb{I}))^n$  by

$$(0.147) \quad g(u_1, u_2, \dots, u_n) \longrightarrow \int g(u_1, \dots, v, u_{i+1}, \dots, u_n) M(u_i, dv).$$

Then the relation (0.144) holds with mutation.

**Example of application** Now consider the case with  $m > 0$ ,  $\mathbb{I} = \{1, 2\}$  as in section 1 and  $\mathcal{F}_0 = 1_1$ . This effect of rare mutation from type 1 to type 2 results in the dual in the transition

$$(0.148) \quad 1_1 \rightarrow 0 \quad \text{at rate } \frac{m}{N}.$$

Returning to our duality relation we now see that the particles in our process  $\eta$  stand for possible individuals, represented by the factor  $1_1$  which could by mutation represent a possible line through which the advantageous type can enter the population. More precisely, if  $\mathcal{F}_0 = 1_1$ , then we can check that as time increases we have an increasing number,  $\Pi_u^{N,1,1}$  of such factors and any of these can undergo the rare mutation transition.

Therefore

$$(0.149) \quad V_t^N = \frac{m}{N} \int_0^t \Pi_u^{N,1,1} du$$

represents the *hazard function* for a rare mutation to occur and therefore  $(1 - \exp(-V_t^N))$  the mean of  $x_2^N(t)$ . Hence the growth of the spatial intensity in the logistic branching particle model relates to the emergence of the rare mutant population.

As a simple application of this dual we can now verify (0.13), (0.14) when there is only one site. In the case  $d = 0$  we have a linear birth process with birth rate  $s$  and therefore  $V_t^N$  grows like  $e^{st}$  and therefore the first rare mutation occurs after a time of order  $O(\frac{\log L}{s})$ . On the other hand when  $d > 0$  the process does not grow indefinitely but approaches an equilibrium. In this case  $V_t^N$  grows only in a linear fashion and therefore requires time of order  $O(L)$ .

We note that since in the process, respectively the dual, time has to be read forward, respectively backward, from  $t$ , the rare mutation jumps occurring in times  $\alpha^{-1} \log N + t$  for the dual after the expansion of the population up to time  $\alpha^{-1} \log N$ , correspond to rare mutations in the original process occurring at times between 0 and  $t$  and then growing till the takeover after time  $\alpha^{-1} \log N$ .

### 3.4 Outlook on set-valued duals

If we consider  $|\mathbb{I}| < \infty$  and use for  $\mathcal{F}_0^+$  *products of indicator functions* we obtain under the evolution *sums of products of indicator functions* where the dynamic of the different summands is coupled by the transition occurring in the underlying process  $\eta$ . Here we briefly describe the main idea how to describe the dual based on a set-valued process but where we introduce the order of individuals and we use a change in the coupling between summands.

To explain the main idea we again consider the case  $\mathbb{I} = \{1, 2\}$ ,  $N = 1$ . Now consider the case

$$(0.150) \quad \mathcal{F}_0 = 1_2.$$

Then at the random time  $\tau$  at which one selection operation occurs we have

$$(0.151) \quad \mathcal{F}_\tau = 1 \otimes 1_2 + 1_1 \otimes 1_2.$$

We can now regard this as defining a subset of  $\mathbb{I}^2$ . If we now couple the transitions in the two summands differently, namely we write instead of (0.151) (this we can do since the dual expression depends only on the marginal law of the summands not the joint law)

$$(0.152) \quad 1_2 \otimes 1 + 1_1 \otimes 1_2,$$

then we can ensure that the summands continue to correspond to *disjoint* subsets of  $\mathbb{I}^N$  and therefore we obtain a dual process with values in subsets of  $\mathbb{I}^N$ .

A much more complicated set-valued dual can be constructed for the general multitype Fisher-Wright diffusion with mutation, selection and migration. The key point is to first take the non-negative function-valued dual driven by the particle system we introduced and then to introduce the *order of factors* and an appropriate *coupling* of its decomposition into a set of summands. This allows us to obtain a duality relation for general finite type space and additive selection with a bounded fitness function.

This duality relation can be interpreted in terms of the *ancestral lines of a tagged sample* of individuals picked from the time- $t$  population, since the dual now gives a decomposition in disjoint events for the ancestral lines and genealogical tree for a tagged sample of  $n$  individuals from the time  $t$  population from which we can read off current types and genealogical distance of the tagged sample.

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